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There and back again: migration in freshwater fishes¹

C. Brönmark, K. Hulthén, P.A. Nilsson, C. Skov, L.-A. Hansson, J. Brodersen, and B.B. Chapman

Abstract: Animal migration is an amazing phenomenon that has fascinated humans for long. Many freshwater fishes also show remarkable migrations, whereof the spectacular mass migrations of salmonids from the spawning streams are the most well known and well studied. However, recent studies have shown that migration occurs in a range of freshwater fish taxa from many different habitats. In this review we focus on the causes and consequences of migration in freshwater fishes. We start with an introduction of concepts and categories of migration, and then address the evolutionary causes that drive individuals to make these migratory journeys. The basis for the decision of an individual fish to migrate or stay resident is an evaluation of the costs and benefits of different strategies to maximize its lifetime reproductive effort. We provide examples by discussing our own work on the causes behind seasonal migration in a cyprinid fish, roach (*Rutilus rutilus* (L., 1758)), within this framework. We then highlight different adaptations that allow fish to migrate over sometimes vast journeys across space, including capacity for orientation, osmoregulation, and efficient energy expenditure. Following this we consider the consequences of migration in freshwater fish from ecological, evolutionary, and conservation perspectives, and finally, we detail some of the recent developments in the methodologies used to collect data on fish migration and how these could be used in future research.

Key words: fish migration, seasonal, evolution, consequences, cyprinids.

Résumé : L'étonnant phénomène des migrations animales fascine les humains depuis belle lurette. De remarquables migrations caractérisent de nombreux poissons d'eau douce, les migrations massives des salmonidés à partir de leur cours d'eau d'origine étant les plus connues et les plus étudiées. Cela dit, des études récentes ont démontré l'existence de migrations chez divers taxons de poissons dulcicoles d'habitats nombreux et variés. Dans la présente synthèse, nous nous penchons sur les causes et conséquences de la migration chez les poissons dulcicoles. Nous abordons en premier lieu les concepts importants et les catégories de migration, puis examinons les causes évolutives qui amènent des individus à accomplir ces déplacements migratoires. La décision d'un poisson donné de migrer ou de demeurer en place repose sur une évaluation des coûts et avantages de différentes stratégies visant à optimiser son effort de reproduction durant sa durée de vie. Nous présentons des exemples basés sur nos propres travaux sur les causes de la migration saisonnière chez un poisson cyprinidé, le gardon (*Rutilus rutilus* (L., 1758)), dans ce cadre. Nous décrivons ensuite différentes adaptations qui permettent dans certains cas à des poissons de migrer sur de grandes distances, dont une capacité d'orientation, l'osmorégulation et l'efficacité des dépenses énergétiques. Nous examinons ensuite les conséquences de la migration chez les poissons dulcicoles des points de vue écologique, évolutionnaire et de la conservation, pour finalement aborder certaines avancées méthodologiques récentes dans la collecte de données sur la migration des poissons et leur utilisation dans le cadre de travaux futurs. [Traduit par la Rédaction]

Mots-clés : migration de poissons, saisonnière, évolution, conséquences, cyprinidés.

1. Introduction

Nothing in [migration] biology makes sense except in the light of evolution (modified from Dobzhansky 1973)

Of all the great spectacles of nature, animal migration is without doubt one of the most remarkable. It has fascinated human-kind for thousands of years, with reports of migratory fishes seasonally moving in and out of the Black Sea being documented over 20 centuries ago (Aristotle circa 350 BC). The study of migration continues to be a major focus of contemporary biological research (e.g., Alerstam et al. 2003; Chapman et al. 2011a), and we now know that migration is a ubiquitous feature in the life cycle of an extremely diverse range of animals, from microscopic crustaceans to large, sea-dwelling mammals (Hansson and Hylander 2009; Horton et al. 2011). There has traditionally been a strong

taxonomic skew in migration studies in favour of avian migration, due in part to the conspicuous seasonal migrations of many birds, and also to the relative ease in observing, marking, and tracking them compared with other animals. Conversely, the migration of aquatic animals such as fishes has received less attention, and so knowledge of migratory patterns in these organisms has lagged behind those of other taxa. Migration in freshwater fishes was previously thought to be relatively rare, as most fish species were considered to be largely sedentary and showing only limited local movement (Lucas and Baras 2001). Notable exceptions to this historical view are of course the salmonids, many of whom make spectacular and highly visible migrations from the sea to their natal habitat, leaping up waterfalls, and congregating in great numbers to spawn in mountain streams (Hendry et al.

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¹This review is part of a virtual symposium entitled "Taxonomic diversity in the biology of migration" that presents a diverse perspective on causes and adaptations of migration in freshwater fishes, mammals, amphibians, and insects.

2004). The migratory behaviour of salmon is also the best-studied example of freshwater fish migration.

Advances in the technologies available for tracking individuals has led to a reassessment of the prevalence of migratory behaviour in the freshwater fishes (Lucas and Baras 2001). Evidence now shows that fishes from almost all freshwater habitats and from all ecological niches make migratory movements at a range of spatial and temporal scales. The improved capacity to gather detailed data on fish movements has also led to a shift from descriptive studies to more hypothesis-driven research aimed to address some of the underlying causes and consequences of migration (e.g., Olsson et al. 2006; Brodersen et al. 2008; Chapman et al. 2011c; Skov et al. 2011).

Understanding patterns of freshwater fish migration is also pertinent in fisheries management, as many commercially important fishes, such as salmonids, are migratory. Furthermore, fish are major players in aquatic ecosystems, and hence, the synchronized movements of often thousands of individuals between habitats can potentially have profound impacts upon ecosystem dynamics (e.g., Brodersen et al. 2008a; Post et al. 2008; Brönmark et al. 2010). Studies of fish migration can also give us clues as to the forces that shape the evolution of migratory behaviour in animals in general, and highlight the fascinating physiological and life-historical adaptations that have assisted individuals in making these periodic journeys between habitats.

In this review we focus on migration in freshwater fishes, beginning with an introduction of concepts and categories of migration, then addressing the evolutionary causes that drive individuals to make these migratory journeys. We then discuss different adaptations that allow fish to migrate over sometimes vast journeys across space. Following this we consider the consequences of migration in freshwater fish from ecological, evolutionary, and conservation perspectives, and finally, we conclude with directions for future research.

1.1. What is migration?

What constitutes animal migration is a matter of some debate, with many definitions in the literature (e.g., Baker 1978; Dingle 2006). Much of the debate reflects the difficulty inherent in classifying the complex and varied movements of a diverse range of animals in the wild. However, most biologists agree that migration requires that individuals or populations (or parts of populations) move between two well-defined habitats on a temporally predictable basis. Hence, migration differs from dispersal in that individuals make a return journey to the initial habitat. The other generally accepted feature of migration is that it is to some degree temporally predictable and has a regular periodicity; for example, the daily vertical movements of pelagic lake dwelling coregonid fish (Mehner and Kasprzak 2011), the seasonal migrations of roach (*Rutilus rutilus* (L., 1758)) from lakes to streams (Brönmark et al. 2008), and also the once-a-lifetime migration of anguillid eels back to their natal marine habitat to spawn and then die (Aarestrup et al. 2009). Throughout the review we follow this definition of migration to maintain a cohesive evolutionary framework as we reflect upon migration and the forces of natural selection that shape migratory behaviours, which may differ to those that shape opportunistic and environmentally responsive movements in fishes, and also dispersal.

1.2. Types of migration

Migratory strategies in nature are diverse, and perhaps especially so among the fishes. Migratory diversity can be addressed in a number of ways, and one can categorize types of migration by function, habitat, and temporal scale or by patterns of movement of the animals themselves. In previous reviews, migration in fishes has mostly been categorized by function, whereby fish

migrate to spawn, take seasonal refuge from predators or adverse environmental conditions, or to feed (e.g., Northcote 1978). Spawning migrations are seasonal and most likely evolved in scenarios whereby the optimal habitat for growth and survival differs between juveniles and adults. Many freshwater fish undertake spawning migrations, for example, the nase (*Chondrostoma nasus* (L., 1758)) that migrates from rivers into tributaries to spawn (Rakowitz et al. 2008). There are also examples in the literature of refuge migrations, where individuals migrate to reduce the risk of predation, often at times of the year when growth potential is reduced (i.e., during winter: Brönmark et al. 2008; Skov et al. 2011). Fish can also migrate to refuge from seasonally adverse environmental conditions, such as low temperature or oxygen. Finally, feeding migrations are common when food resources fluctuate in a predictable manner across time and space.

A second way to classify fish migration is by habitat. Many fishes migrate between freshwater and marine habitats, which is known as “diadromy”. Diadromy can be further divided by whether a fish migrates from freshwater to marine habitats (“anadromy”), or from marine to freshwater habitats (“catadromy”). Anadromy is thought to be more common than catadromy and is widespread in well-studied groups such as salmonids, which migrate as juveniles from streams to the ocean, returning to spawn often in the same stream where they were born (Hendry et al. 2004). A classic example of catadromy is the European eel (*Anguilla anguilla* (L., 1758)), which migrates from its natal habitat in the Sargasso Sea to spend its adult life stages in the rivers and lakes of Europe, before making the return journey to reproduce and then die (Aarestrup et al. 2009). Migration between two freshwater habitats is known as “potamodromy” and is less well studied (but see Northcote 1997). Potamodromous fishes may migrate from lakes to streams, as is the case with roach, common bream (*Abramis brama* (L., 1758)), and white bream (*Blicca bjoerkna* (L., 1758)) (Skov et al. 2008), or may make migrations to different areas of river habitats, as do predatory pikeperch (*Sander lucioperca* (L., 1758)) (Koed et al. 2000). Finally, fish that migrate between marine habitats are known as “oceanodromous” migrants. While these latter migrations are both fascinating and increasingly studied, they are beyond the scope of our review and we direct interested readers to other reviews on this subject (e.g., Metcalfe et al. 2008).

Migrations can also be classified according to the temporal scale over which migratory cycles occur. Most freshwater fish migrations are “seasonal”, and population movements occur in response to changes to seasonal shifts in food availability, predation risk, or to spawn in habitats optimal for juvenile growth and survival. However, a number of fish species perform migrations at a much smaller temporal scale. “Diel vertical migration”, where fish migrate up and down the water column has been shown to occur in a number of freshwater fish species (Mehner 2012). For example, juvenile Bear Lake sculpin (*Cottus extensus* Bailey and Bond, 1963) of <30 mm in length spend the day at the bottom of lakes and then vertically migrate 30–40 m to the surface waters during the night (Neverman and Wurtsbaugh 1994). Furthermore, many fish species perform a “diel horizontal migration”, where they migrate from the littoral zone of lakes into offshore areas at dusk and then return to the littoral zone at dawn (e.g., Gliwicz et al. 2006; Muška et al. 2013).

A final way of categorizing migratory behaviour in fishes is based upon describing migratory variation between individuals from the same population. “Differential migration” refers to cases where individuals within populations differ in their migratory behaviour in some way, such as in their destination or direction of movement, in their timing, or in their propensity to migrate (Newton 2008). For example, it has been shown that male and female salmon differ in the timing of their migration to the sea (Jonsson et al. 1990), and some males may even stay the whole life cycle in the natal stream, adopting an alternative life-history strategy (so called “sneaker males”; Fleming 1996; Dodson et al.

2013). Variation in the destination of migratory fish has been shown in populations of roach migrating seasonally from shallow lakes into connected streams during winter. Migratory roach from Lake Krankesjön in southern Sweden migrated into different streams, and for many individuals their destinations were consistent over a number of years (Brodersen et al. 2012). There are also many examples of fish populations that do not migrate in their entirety, a phenomenon known as “partial migration” (Chapman et al. 2011a, 2011b). Recent reviews highlighted that partial migration is widespread in freshwater fishes and that many populations are composed of a mixture of migrant and resident individuals (Chapman et al. 2012a, 2012b). As we become more able to track individual animals as they migrate across space and time, it seems clear that differential migration is the rule rather than the exception and that significant variation exists in migratory behaviour within populations.

1.3. Which species migrate?

Migration has been increasingly documented in a diverse array of families of freshwater fishes. Besides the iconic examples of salmonid and eel migration, we now know that species from many other taxa also show migratory behaviour. Among the cyprinids, for example, a group that were until only recently thought to be mostly sedentary in their movements, migration between lakes and streams has now been reported in white bream, common bream, and roach (Skov et al. 2008). Anadromy has also been documented in this group. There has also been some geographical bias in studies of fish migration, meaning that most research focus has been directed to European and North American freshwater fishes. As studies proliferate in the tropics and in the southern hemisphere, the prevalence of migration in freshwater fishes becomes increasingly obvious. We direct interested readers to detailed taxonomic reviews (Lucas and Baras 2001; Chapman et al. 2012b).

Given that migration is so widespread among freshwater fishes, it appears that there are few phylogenetic constraints on the evolution of this fascinating behaviour. From an evolutionary perspective, migration has evolved as an adaptive strategy to maximize individual fitness, as individuals migrate to increase their growth, survival, or reproductive success. In the following section we discuss the ecological factors that play a role in the evolution of freshwater fish migration. We of course acknowledge that studies on salmonid migration have been instrumental in our understanding of migration in fishes and, hence, any review of the migration of freshwater fishes has to rely heavily on research performed on this group. However, we will try to add to the picture by also including studies on other taxa, to increase generality, but also because of our own research bias towards migration in cyprinids.

2. Why migrate? Evolution of migration in freshwater fish

Traditionally, the study of migration in fishes was mainly concerned with describing migration trajectories and the environmental factors that act as proximate cues for migratory behaviour, but in recent years there has been more and more focus on the ultimate causes behind migration, i.e., the factors involved in the evolution of different migration strategies (Dodson 1997). Here, it is important to emphasize that although these spectacular mass migrations in fish involve a huge number of individuals, the decision to migrate or not is made by the individual and it is made as part of an adaptive strategy to maximize lifetime reproductive effort. The basis for this decision is an evaluation of the costs and benefits of different strategies, i.e., evolution of migration is expected when the fitness benefits of migrating between habitats minus the migration costs exceeds the fitness of a resident strategy (e.g., Gross 1987). To exemplify the powerful approach of cost–

benefit analyses for understanding the evolution of migration in fish at a range of different spatial and temporal scales, we will highlight three examples: anadromous migrations between freshwater and marine habitats in salmonids, seasonal migration between lake and stream habitats in cyprinids, and lastly, diel vertical migrations within lake systems in ciscoes.

2.1. Anadromy in salmonids

The evolution of diadromous migration patterns has been coupled to different costs and benefits (e.g., Gross 1987; Hinch et al. 2005) and is especially well studied in anadromous salmonids. Salmon that migrate to the ocean have been suggested to benefit by being able to exploit the rich food resources in the sea, resulting in a higher growth rate than if they had stayed in the freshwater habitat. A large size at maturity affects fitness, as the fecundity and (or) egg size of larger females is greater (e.g., Morita and Takashima 1998) and, furthermore, larger males are more successful in the competition for females at the spawning grounds (Quinn and Foote 1994). Migration may also reduce the exposure to predators and parasites and, furthermore, decrease the risk of mortality that is due to adverse abiotic conditions (e.g., hypoxia) in the small spawning streams. However, migration also comes with different costs, where the most evident probably is the energetic cost of the migratory movement itself (see below). There are also developmental costs for specific migratory adaptations, including changes in osmoregulation when moving into the marine, saltwater habitat. It has also been suggested that predation risk en route and at sea is higher than in the freshwater habitat, and hence, migration may result in an increase in mortality rates (Gross 1987; Northcote 1997).

2.2. Seasonal migration in cyprinids

Migration may also occur in a strictly seasonal pattern, i.e., all or parts of the individuals in a population migrate repeatedly every migration season. In the last decade our research group has focused on the causes of seasonal migration of cyprinid fish between shallow lakes and streams. To understand the mechanisms behind the seasonal migration in cyprinids in shallow lakes, we developed a conceptual model (Brönmark et al. 2008) that was based on Werner and Gilliam's (1984) theoretical framework for habitat choice in organisms exposed to conflicting demands. Several studies have suggested that this general framework may be useful in understanding the evolution of migratory behaviour in fish (Clark and Levy 1988; Jonsson and Jonsson 1993; Schindler 1999; Tarling et al. 2000; Borchert et al. 2002). Our model suggests that seasonal migration in fish is an adaptation that has evolved in response to seasonal changes in habitat-specific predation risk (P) and growth (G). Thus, cyprinid fish should shift habitat so as to minimize the P/G ratio and, consequently, they should leave the lake in autumn and return in spring (Brönmark et al. 2008). We PIT-tagged (passive integrated transponders) a large number of fish, mainly roach and common bream, in the lake. Migrating roach and common bream are mainly zooplanktivorous and benthivorous, respectively, in this lake and their main predators are piscivorous fish (northern pike, *Esox lucius* L., 1758; European perch, *Perca fluviatilis* L., 1758) and birds (Great-crested Grebe, *Podiceps cristatus* (L., 1758); Great Cormorant, *Phalacrocorax carbo sinensis* (Blumenbach, 1798)) (C. Brönmark, K. Hulthén, P.A. Nilsson, C. Skov, L.-A. Hansson, J. Brodersen, and B.B. Chapman, unpublished data). Recording stations placed in the inflow and outflow streams allowed us to follow the seasonal migration patterns of tagged fish and we could thereby test our predictions empirically. We found that a large proportion of cyprinid fish, mainly roach and common bream, migrated from the lake into the streams in October and back to the lake in April (Skov et al. 2008). The timing of the migration followed our predictions with remarkable accuracy (Brönmark et al. 2008), suggesting that

migration patterns have evolved in response to seasonally fluctuating trade-offs between predator avoidance and foraging gains. Furthermore, it is also notable that the dominant zooplanktivore, roach, is actually absent from the lake during a major part of the year, which should have strong implications for the dynamics of the lake ecosystem through direct and indirect food-web interactions (see below).

Our model predicts migration patterns at the population level, but could also be used to understand migration strategies leading to partial migration, i.e., where a part of the population migrates and the others are resident. Such differences in migratory propensity among individuals within a population may be due to differences in individual traits, such as size or condition, which affect the P/G trade-off at the individual level (e.g., Olsson et al. 2006; Brodersen et al. 2008c; Skov et al. 2011). Fish are commonly exposed to predation from gape-limited predators such as piscivorous fish (Nilsson and Brönmark 2000). Thus, smaller prey fish individuals have a higher risk of predation mortality (P) and should hence migrate to a greater extent than larger individuals. This was tested in a study of common bream migration in Danish lakes (Skov et al. 2011), where we found that migration probability increased with increasing individual vulnerability to predation because small individuals at high risk of predation had a higher probability of participating in migration than large, low-risk individuals (Skov et al. 2011). This suggests that individual differences in predation risk may explain polymorphisms in migratory behaviour resulting in partial migration. The effect of differences in predation risk for migratory propensity was also evidenced in a study of the importance of personality traits for migration in roach. Bolder individuals, which should be more at risk to predation than shy individuals, were more likely to migrate from the lake to the stream during winter (Chapman et al. 2011c). In the studies above we highlighted the importance of piscivorous fish, mainly pike, as the predators driving the seasonal migration patterns in cyprinids. However, in a recent study we showed that predation by cormorants may also impose a substantial risk of mortality (Skov et al. 2013). Predation rate by cormorants was significantly higher on resident than on migrating roach, i.e., we have here been able to show that migration incurs a significant benefit by reducing the cost of predation.

Differences in growth rate among individuals may also affect the P/G ratio and the propensity to migrate. Differences in growth rate among individuals affect their condition, i.e., partial migration can be seen as a result of two condition-dependent alternative strategies: either stay in the lake with a relatively higher predation risk or migrate to the stream that has low food availability and low density of piscivores. For well-fed fish it is beneficial to migrate and reduce predation risk, whereas for fish in poor condition it is better to stay in the lake, despite a higher risk of predation, to feed and improve their condition and thereby decrease the risk of starvation. In an experimental study where we manipulated the condition of roach before the migration period, we indeed found that migration is condition-dependent because well-fed individuals in high condition migrated to a larger extent (Brodersen et al. 2008c). Further support for this idea can be found in a recent study that quantified a feeding cost to migration in roach (Chapman et al. 2013).

2.3. Diel migrations

Fishes have also been shown to migrate on shorter time and spatial scales than in the seasonal migrations described above. In lakes, fish have been shown to perform diel vertical migration (DVM), where they typically spend the daytime in the deeper layers and then migrate to shallower depths at night (Mehner 2012). This has been suggested as a strategy to increase bioenergetic efficiency, where fish capitalize on the differences in temperature between deep and shallow waters and choose depths so as to

maximize their growth rate (e.g., Neverman and Wurtsbaugh 1994). However, it has also been suggested that DVM is driven by a habitat specific trade-off between predation risk and feeding opportunities (e.g., Scheuerell and Schindler 2003; Hrabik et al. 2006), similar to the argument for seasonal migration discussed above. Prey fish should thus migrate to the dark, deeper layers during daytime to avoid predation by visually oriented piscivores and then return to the shallow depths during night to feed on zooplankton. Visually hunting piscivores have a higher light threshold for efficient foraging than fishes that use vision when foraging on zooplankton (Giske and Salvanes 1995) and it has been suggested that ascending fish utilize this asymmetry to prolong their feeding time by moving within an “antipredation window”, i.e., they are feeding in water layers where there is enough light for selective feeding on zooplankton, but not enough for efficient foraging in visually hunting piscivores (Clark and Levy 1988; Scheuerell and Schindler 2003). The DVM of freshwater fish has typically been described as a population phenomenon (i.e., all of the individuals in the population migrate), but recently a study of two cisco species (vendace, *Coregonus albula* (L., 1758); Fontane cisco, *Coregonus fontanae* Schulz and Freyhof, 2003) demonstrated that the DVM in these species was partial (Mehner and Kasprzak 2011). Furthermore, the onset and speed of migration was size-dependent with smaller fish ascending earlier and faster (Busch and Mehner 2012), which was argued to be due to individual differences among fish balancing foraging gains, predation risk, and reproductive value.

Recent studies have also suggested that habitat-specific trade-off between predation risk and feeding opportunities drives the diel “horizontal” migration (DHM) that is common in many lake fish (e.g., Gliwicz et al. 2006; Muška et al. 2013). Here, fish migrate at dusk from the littoral to the offshore pelagic zone to forage on zooplankton and then at dawn they return to the complex littoral habitats that provide a predation refuge. Gliwicz et al. (2006) found that only a fraction of a roach population left the daytime refuge at dusk (i.e., a partial migration), but argued that an individual that had stayed in refuge one night should take the risk of foraging offshore in the high-food, high-risk area. Increasing volumes of food in the guts of roach caught at increasing distances from the shore also suggested the high benefit of foraging far from the refuge area in the littoral. Furthermore, Muška et al. (2013) found that the DHM in common bream and roach was size-dependent, such that larger individuals stayed in the risky offshore habitat also during day, whereas juvenile and small fish migrated to the safer littoral zone at dawn. Thus, patterns in both DVM and DHM again highlight the necessity to evaluate different selection pressures operating simultaneously and at the individual level to understand the evolution of different migration strategies.

3. Adaptations for migration

For a diverse array of animals, migration constitutes one of the most demanding events in the life cycle (Dingle 1996). To cope with the hardships during their arduous journeys, migrants parade an impressive suite of fine-tuned adaptations that act in concert to promote migratory behaviour. Many morphological, physiological, and behavioural traits correlated with migratory behaviour seem to be shared across migrants as diverse as birds, fish, and insects (Dingle 2006; Ramenofsky and Wingfield 2007). Below we review some of the adaptations that facilitate migration in freshwater fishes, especially in the salmonids, as a majority of studies on migratory adaptations so far has focussed on this group.

3.1. Orientation

Many freshwater fishes show complex migration patterns, as described above. This can be exemplified by salmon that migrate

to sea as juveniles and then return to freshwater habitats to spawn, in many cases to the exact stream, and even stretch within the stream, where they were born. The return to their native habitat may be regarded as an adaptive behaviour, as they return to a site where spawning obviously has been successful. Homing to native streams also results in low gene flow among neighbouring populations and this allow for the evolution of populations that are locally adapted to the specific environment of their home stream (Taylor 1991; Dittman and Quinn 1996; Hendry and Quinn 1997), resulting in, for example, population differences in body morphology (see below). Also, migrating cyprinids show some degree of site fidelity, both during spawning migrations (L'Abée-Lund and Vøllestad 1987) and during winter migrations (Brodersen et al. 2012), but whether this is due to local adaptation or simply individual behavioural consistency (as demonstrated in Brodersen et al. 2012) is yet unknown. The link between local adaptation and migratory site fidelity could, however, easily be imagined to be a general pattern for many types of fish migrations.

During their oceanic stage, salmonids may disperse over huge geographic regions in the sea and the obvious question is of course: how do they find their way back to their native stream from these far away distances and after several years at sea? This intriguing question may be split into two additional questions. First, how do fish orient at sea? And second, how do they locate their natal stream?

Orientation at sea is still very much an open question, although a number of mechanisms have been proposed. The fact that salmonids converge at the mouth of their natal river at the start of the spawning season suggests that they have a complex map and compass system that allows them to navigate with great temporal and spatial precision (e.g., Dittman and Quinn 1996). Different sensory mechanisms for accurate orientation have been suggested, including orientation using sun position, polarized light patterns, and the Earth's geomagnetic field (Quinn 1980). Polarized light may provide a good orientation cue for fishes that migrate at sunrise–sunset when the polarized light patterns are strongest (Quinn and Ogden 1984). A response to geomagnetic cues has been shown in some species (Walker et al. 1997) and biogenic magnetite crystals have been found in the olfactory lamellae of rainbow trout (*Oncorhynchus mykiss* (Walbaum, 1792)) (Walker et al. 1997) and in the lateral line of Atlantic salmon (*Salmo salar* L., 1758) (Moore et al. 1990). A recent analysis of a long-term fisheries data set suggested that sockeye salmon (*Oncorhynchus nerka* (Walbaum, 1792)) from Fraser River are imprinted by the magnetic field when they migrate to sea and that they use differences in magnetic-field intensity to efficiently locate the coastal imprinting site during their return migration (Putman et al. 2013). However, the map and compass theory is not undisputed. Døving and Stabell (2003) (see also Stabell 2012) argued that compass orientation is impossible in fish because they lack a biological clock that is accurate enough and instead they use their well-developed olfactory system to orient to their natal stream.

Although there has been and still is much debate on what sensory cues fish use to migrate in the open sea, it has been clear for some time that salmonids use olfaction to distinguish among different streams (e.g., Hasler and Wisby 1951). Two major hypotheses explaining the olfactory cues have been proposed, the “olfactory imprinting hypothesis” (Hasler and Wisby 1951) and the “pheromone hypothesis” (Nordeng 1971). The imprinting hypothesis suggest that each stream has a characteristic composition of chemical substances originating from the surrounding soil and vegetation creating a stream, and even site-specific, odour that is imprinted on the juvenile. It is this “stream bouquet” that the salmonids may use as olfactory cues in their homeward migration from the sea. The pheromone hypothesis, in turn, suggests that the migrating adults use population-specific pheromones that are released by juvenile relatives in their natal stream. In petromyzontid lampreys, it has been shown that adults use bile acid pher-

omones from juvenile lampreys to locate spawning streams (Fine et al. 2004), but these cues provide species-specific cues only; adult lampreys do not home to their natal stream.

3.2. The energetics of migratory behaviour

Fish show a remarkable diversity of migratory behaviours and migration is accompanied by costs in time, energy, and risk that vary with the distance travelled and the hardships encountered (Bernatchez and Dodson 1987). Massive fuelling on the feeding habitats followed by migration in a fasting state (i.e., on a fixed energy budget) is the hallmark of many anadromous species, including Pacific salmon (*Oncorhynchus* spp.), Atlantic salmon, and American shad (*Alosa sapidissima* (Wilson, 1811)), and appears to be similar for cyprinids migrating from lakes to streams in winter (Brodersen et al. 2008c). Once in the natal river, returning anadromous salmonids may struggle for weeks against falls and rushing rapids and a substantial part of the initial energy reserves may be depleted (Glebe and Leggett 1981; Brett 1995), potentially contributing to en route and prespawning mortality (Rand and Hinch 1998; Rand et al. 2006). This is especially important for migrants with a semelparous life history, such as Pacific salmon, because they die after reproduction and thus achieve their total lifetime fitness via this single reproductive event. In addition to direct mortality, migratory costs may also be manifested as decreased fecundity and studies have reported negative correlations between fecundity and migration distance in several fish species (e.g., Beacham and Murray 1993; Kinnison et al. 2001; Crossin et al. 2004). More evidence in support of the idea that demanding migrations have negative impact on fitness parameters comes from a study involving numerous resident and migratory populations of brown trout (*Salmo trutta* L., 1758). Bohlin et al. (2001) elegantly revealed a more rapid decrease in juvenile fish density with increased elevation among anadromous populations compared with resident populations. Furthermore, Crossin et al. (2004) compared fuel loads in migrating populations of sockeye salmon and found that populations which undertake long-distance migrations or home to natal rivers at high altitude initiated upriver migration with more somatic energy and fewer eggs. A cross-species comparison of the energetic costs involved in migration for 15 anadromous populations from nine different species showed that long-distance migrants tended to be more energy efficient compared with short-distance migrants and only populations that need all their energy to successfully complete migration swam at speeds close to the theoretical optimum (Bernatchez and Dodson 1987). With regards to migration efficiency, some evidence also suggests that fish migrants, both salmonids and cyprinids, may actually take stream current velocity and tidal cycles into account to minimize transportation costs (Levy and Cadenhead 1995; Brodersen et al. 2008b; McElroy et al. 2012).

For species with an iteroparous life-history strategy, it is of great importance to spend available energy reserves so as to ensure future survival and reproduction. A study of American shad showed that populations with a high frequency of repeat spawners (individuals return to the sea between reproductions) invested less in migration and reproduction compared with conspecific populations with a semelparous strategy (Glebe and Leggett 1981).

The catadromous European eel, one of the most spectacular fish migrants, undertakes an extreme (5000–6000 km) spawning migration from Europe to the Sargasso Sea in a fasting state; a journey that takes several months to complete (Tesch 2003; Aarestrup et al. 2009; Righton et al. 2012). Eels deposit lipids as the primary energy reserve and have been proposed to depart towards the spawning grounds when the fat reserve exceeds a threshold level (Boetius and Boetius 1985; Larsson et al. 1990). Migrating silver eels have been shown to carry fuel loads with fat reserves ranging from 10% to 28% (Svedäng and Wickström 1997). The low fat contents found in some migrating silver eels have provoked

controversy and debate as to whether the fuel load carried by migrating eels is sufficient to power the long-distance migration and subsequent spawning in the Sargasso Sea. However, in a landmark study, [van Ginneken et al. \(2005\)](#) shed light on the remarkable migratory capability of eels by simulating the migration (5500 km over 173 days) in swim tunnels. European eels are indeed extreme endurance migrants that swim 4–6 times more efficiently than non-anguilliform fish and seem to carry sufficient fuel loads to accomplish a trans-Atlantic migration and still have significant amounts of energy left to devote to gonadal development ([van Ginneken and van den Thillart 2000](#); [van Ginneken et al. 2005](#)).

3.3. Morphological correlates of migration

The shape of a fish is strongly associated with hydrodynamic performance and morphological traits such as a streamlined body can significantly reduce drag (e.g., [Webb 1984](#)) and thereby facilitate swimming during migration. Morphological adaptations for migration in fish have been extensively studied in salmonid migrants. Two key characteristics in the smoltification process are a marked increase in body length relative to mass resulting in streamlining of the body ([McCormick et al. 1998](#)) and a decrease in relative size of pectoral fins. These morphological modifications are presumably adaptive for migratory performance. Furthermore, variations in body morphology may also occur as a result of adaptation to local conditions and several studies have shown correlates of body morphology with migration distance and hydrologic conditions in the natal habitat (for a review see [Taylor 1991](#)). For example, [Crossin et al. \(2004\)](#) compared the morphology of short- and long-distance migratory populations of Fraser River sockeye salmon and showed that populations which make difficult migrations had short, fusiform bodies that are favourable for reducing transportation costs. Similarly, brook charr (*Salvelinus fontinalis* (Mitchill, 1814)) populations that undertook longer migrations were more adapted for energy-efficient migration with more streamlined bodies and longer caudal regions ([Fraser and Bernatchez 2005](#)). Further evidence that long migratory routes may impose significant selection pressures on morphological features comes from a cross-population comparison of Atlantic salmon ([Fraser et al. 2007](#)). Body shape was a significant predictor of migration distance with long-distance migrants being more streamlined.

Many species show large intraspecific variation in morphology and can form distinct alternative morphological phenotypes (e.g., [Moran 1992](#)), but rarely has this been related to migration in non-salmonids (notable exceptions are the alewife, *Alosa pseudoharengus* (Wilson, 1811) ([Jones et al. 2013](#)), and the three-spine stickleback, *Gasterosteus aculeatus* L., 1758 ([Jones et al. 2006](#))). We are, however, convinced that morphological adaptations to migration will be described for many other species in the future. However, morphological correlates of migration should not automatically be regarded as adaptive for the migratory travel per se. Many traits found in migratory fish may be an adaptation to increase performance in the alternative habitat rather than to increase performance during migration. For example, development of a kype (a hook-like jaw) in migratory salmonids is increasing reproductive output ([Fleming 1996](#)), but appears unlikely to be adaptive for migration.

3.4. Crossing the interface: osmoregulation

Needless to say, diadromous migrations between discrete environments (i.e., hypo-osmotic freshwater vs. hyper-osmotic seawater) place enormous demands on osmoregulatory ability. All fish migrants that cross the interface between freshwater and saline habitats must therefore undergo physiological changes ([Hinch et al. 2005](#); [Righton et al. 2012](#)). Diadromous migratory behaviour and the capacity to adapt and survive in habitats that

differ in salinity are widespread and have been documented in a diverse range of fish species, from Atlantic salmon to pike ([Chapman et al. 2012b](#)). However, preparatory physiological adaptations (smoltification) that occur well before the transition to marine habitats differentiate salmonids from other species with euohaline capability ([Stefansson et al. 2008](#)). Although smoltification involves the integration of multiple regulations, the increase in euohalinity is a key characteristic and perhaps the most critical element given the modest osmoregulatory ability of the stream dwelling parr ([Stefansson et al. 2008](#)). Major functional changes in important osmoregulatory organs such as the gill, kidney, gut, urinary bladder, and skin occurs before the transition between the marine and freshwater environment (for details involved in salmonid osmoregulation see, e.g., [Clarke and Hirano 1995](#); [McCormick and Saunders 1987](#)).

4. The genetics of migration

A significant amount of the phenotypic variability in migratory traits in migrating animals is most likely under genetic control, but the genes involved are poorly understood ([Liedvogel et al. 2011](#)). The classic approach to disentangle the genetic component of behaviours, i.e., local adaptations to specific selective environments, is by performing either translocation or common garden experiments. Such studies have also provided insight into the genetic component of migratory behaviour in freshwater fish. For example, in a translocation experiment migrating individuals of a cyprinid (roach) were moved to an unfamiliar habitat and their behaviour compared with the local population ([Skov et al. 2010](#)). The majority of fish in the translocated, nonlocal populations initiated their migration several weeks before the majority of the individuals of the local population, indicating a genetic component in the timing of migration in this species ([Skov et al. 2010](#)). Another example indicating the role of genetics in shaping inter-population phenotypic differences in migratory behaviour comes from a study on Atlantic salmon ([Plantalech manel-la et al. 2011](#)). Here the authors used a common garden approach to show that fish from two populations had consistently different migration behaviour when stocked in an unfamiliar environment. One population had a short migration distance from their natal river to the sea, whereas the other had a long migration distance. When stocked into an unfamiliar environment that had a long distance to the sea, the latter population had faster migration and better survival than the population with no experience of long migration distances. Based on this, the authors further suggest that selective pressures of marine predation and arrival time at feeding areas in the ocean may be stronger for stocks with a longer inshore migration, creating more efficient migrants over time ([Plantalech manel-la et al. 2011](#)).

The development of functional genomics has resulted in a new and powerful tool that could be used to study the genetics behind migratory behaviour. Studies on salmonids have already identified genes with different expression patterns between resident and migratory individuals pre-migration ([Giger et al. 2008](#)). Transaldolase 1 and endozopine are expressed at lower levels in potamodromous and anadromous individuals compared with resident individuals ([Amstutz et al. 2006](#); [Giger et al. 2006, 2008](#)). In addition, [Aubin-Horth et al. \(2009\)](#) found differences in gene expression between Atlantic salmon males adopting different life-history strategies (for a recent review of alternative migratory tactics in salmonids see [Dodson et al. 2013](#)). Sneaker males, i.e., males that are resident in the stream and become mature at an early age and smaller size, showed up-regulation of genes involved in the endocrine reproductive pathway and in genes associated with learning and memory. In migrating males, on the other hand, genes associated with regulation of thyroid hormones were up-regulated, which was suggested to be a prepara-

tion for the transition to the saltwater habitat. There were also differences in gene expression between early- and late-migrating males. Similar results have been found for anadromous and freshwater resident forms of three-spine stickleback (for a review see [Kitano et al. 2012](#)). Further, studies on Pacific salmon (*Oncorhynchus* spp.) have suggested that clock genes are involved in determining the timing of spawning (and thus migration) among populations at different latitudes and that variation at this gene is shaped by selection ([O'Malley and Banks 2008](#); [O'Malley et al. 2010](#)). Gene expression studies can also be used to optimize management decisions as has been convincingly shown by [Miller et al. \(2011\)](#). They used a combination of watershed-scale biotelemetry and gene expression to investigate the collapse of wild sockeye salmon in the Fraser River, Canada. Based on an identification of a common genomic profile for this species, they were able to explore potential physiological mechanisms that could be associated with survivorship during return migration. Based on this the authors suggested that the elevated mortality in recent years is caused by a virus which infects the fish before they enter the river to spawn.

The role of genetics in migration is also exemplified by current discussions of the interplay between partial migration and genetics. In a recent review, [Pulido \(2011\)](#) advocates that migration has a genetic basis, but whether this genetic variation is expressed or not, and if so, how strongly, is determined by the environment. The model assumes that there is a normally distributed trait called liability, which underlies the expression of a dichotomous trait (i.e., to migrate or not), and a threshold, through which the phenotype of the dichotomous trait is produced. If the liability of an individual is above the threshold, then the trait will be phenotypically expressed, i.e., the individual will migrate ([Pulido 2011](#)). This environmental threshold model predicts that facultative and obligate partial migration, as well as residency and complete migration, are all controlled by the same mechanisms. Although [Pulido \(2011\)](#) based most of his argument on studies of bird migration, he suggested that this threshold mechanism could account for migration in fish as well and use salmonids as an example, i.e., migration in salmonids could be regulated by a migration threshold and a liability which is correlated to body size at a particular age ([Páez et al. 2011](#)).

5. Consequences of migration

In the study of fish migrations we often distinguish between causes and consequences, or alternatively, mechanisms and effects. For example, we may categorize food availability or predation risk as driving causes of migration (e.g., [Brönmark et al. 2008](#)), whereas decreased competition or change in trophic dynamics may be classified as consequences of migration (e.g., [Brodersen et al. 2008a, 2011](#)). As fish have multiple important roles in freshwater ecosystem, the temporal presence-absence and movement between habitats are likely to have multiple effects on their surrounding ecosystems. These effects can be divided into the three categories: (1) redistribution of nutrients, (2) food-chain effects, and (3) eco-evolutionary effects. Whereas within-population effects of migration are likely to occur irrespective of the importance of the migratory species in the ecosystem, significant trophic effects mediated through ecosystem interactions most likely requires the migratory species to be either a keystone or a dominant species in the ecosystem. Alternatively, the migration can be carried out by multiple species with an additive effect on the ecosystem. Lastly, the migratoriness of a species may have an influence on biogeographic dynamics, i.e., the likelihood of invading new habitats, but since this is poorly described in the scientific literature, we will leave this subject for future discussions.

5.1. Redistribution of nutrients through fish movements and migrations

Ecosystems and biomes are not closed entities. Transport and flow of substances and nutrients are common both within and between systems. Nutrients such as phosphorus, nitrogen, and carbon are structural and functional fundamentals in all organisms and are therefore associated with important features in food webs and ecosystems. Their distribution within and between habitats is affected by a multitude of factors, among them by migrating organisms. Hence, some of the major ecosystem consequences of migration are redistribution of nutrients. In this section we will address how migratory fish may affect nutrient flows both within different freshwater habitats and between freshwaters and the ocean.

One of the most well-known and spectacular phenomena among fish is the ontogenetically driven migrations of the salmon and trout species complex of the Pacific Northwest of North America ([Naiman et al. 2002](#); [Schindler et al. 2003](#)), where fish are born in lakes, migrate to sea as juveniles, and then grow tremendously in size based on marine resources. When ready to spawn they migrate in enormous amounts back to their natal lake, where they spawn and die. Hence, carcasses deliver considerable amounts of phosphorus, nitrogen, etc. and the whole food web of these lakes is affected by this ocean subsidy ([Naiman et al. 2002](#); [Wilcove and Wikelski 2008](#)). The nutrients released by the dead fish are absorbed by phytoplankton, which are then eaten by zooplankton, which, in turn, constitute suitable food packages for zooplanktivorous fish, including newly hatched salmon larvae! Furthermore, salmon eggs provide a considerable nutrient source for rainbow trout and arctic grayling (*Thymallus arcticus* (Pallas, 1776)), which may increase their feeding rate with up to four times during the egg laying period of salmon ([Scheuerell et al. 2007](#)).

Although commonly noted as a potential phenomenon that may affect the productivity of lower trophic levels in the oligotrophic lake ecosystems used for spawning ([Leavitt et al. 1994](#); [Schindler et al. 2001](#)), this nutrient transport from the sea is rarely quantified. However, [Moore and Schindler \(2004\)](#) estimated the phosphorus transport by sockeye salmon from the ocean to four Alaskan lakes to be between 10 and 100 tonnes per year. In an attempt to quantify the overall fish effect on nutrient dynamics, [Schindler et al. \(2001\)](#) estimated the phosphorus regeneration rates to be 3.3 and 1.7 mg phosphorus·m⁻³·year⁻¹ in lakes currently stocked with trout compared to unstocked lakes, respectively. This doubling in phosphorus regeneration was used by phytoplankton, which responded with an almost 10-fold increase in biomass as estimated from paleolimnological data ([Schindler et al. 2001](#)). Hence, marine-derived nutrients strongly affect the primary producers in freshwaters and historical changes in lake algal production is linked with salmon population dynamics ([Brock et al. 2007](#)). Such time-series observations are strengthened by the observation that the development of commercial fishing around 1890 was associated with a considerable reduction in algal production in lakes ([Schindler et al. 2005](#)). The mass migration between the ocean and freshwater biomes has decreased considerably as a result of anthropogenic influences ([Wilcove and Wikelski 2008](#)), resulting in that only about 6%–7% of the historical nutrient subsidies are now provided by the ocean through this migratory route ([Gresh et al. 2000](#)).

Nutrients are, however, not only transported from the ocean to freshwaters, but also in the other direction through smolt that migrate from the lake to the ocean ([Moore and Schindler 2004](#)). With respect to nutrient transport this migration constitutes <15% of what adult salmon carry to freshwaters, i.e., over time there is a net transport of nutrients from the sea to freshwaters ([Moore et al. 2011](#); [Moore and Schindler 2004](#)). Studies on migrating sockeye salmon in Alaskan streams have also assessed the transfer of marine-derived nitrogen to terrestrial systems via emerging aquatic insects ([Francis et al. 2006](#)). However, compared with the total amount of nitrogen

transported by salmon from the ocean, insects only transferred about 0.03% to terrestrial food webs, i.e., insects might not be major vectors for nutrient transport from the ocean, via freshwaters to terrestrial systems.

Fish migrations may also redistribute nutrients within lakes. Many fish taxa perform diel vertical migrations by feeding in deep, cool waters during the day and resting in warmer surface waters during the night (Mehner 2012). Hence, schools of coregonids will ingest zooplankton in deep strata during the day and excrete nutrients through feces in the upper strata during the night. Similarly, fish that migrate horizontally may move nutrients from the pelagic to the littoral zone. We may conclude that at the global and regional scale, the mass migrations of the salmon–trout complex move considerable amounts of nutrients over long distances, albeit only during short periods of time. At the local scale, however, fish migrations between habitats within a system may redistribute small amounts of nutrients over short distances. However, those small-scale transports of nutrients are continuous, i.e., are ever ongoing phenomena, which potentially makes them important within many aquatic ecosystems.

5.2. Food-chain effects

It is inherent to migration that animals move over and between areas, and consequently, their ecological roles also move over time and space. Since migrants, just as any animals, both consume resources and constitute prey to predators, migration may affect the strength of consumer–resource interactions and thus have effects on the trophic interactions in the communities they are migrating to and from, respectively (Brodersen et al. 2008a; Post et al. 2008). Trophic interactions are very important drivers of the structure and dynamics of aquatic systems and it is hence not only important to consider how environmental circumstances may drive fish migration, but also how fish migration feeds back on and affects the aquatic environment.

Fish predation can have cascading and far-reaching consequences in aquatic food chains, potentially affecting ecosystem composition and function (Carpenter and Kitchell 1993). For instance, size-selective predation by zooplanktivorous fish affects the biomass and size structure of zooplankton, which in turn affect the grazing rates zooplankton exert on phytoplankton communities, resulting in a trophic cascade from fish to phytoplankton (e.g., Hansson 1992; Carpenter and Kitchell 1993). Similar top-down effects have been shown in benthic food chains involving benthivorous fish, grazing snails, and periphyton (e.g., Brönmark et al. 1992). Changes in the density of planktivorous or benthivorous fish thus have the potential to affect the strength of the trophic cascade and below we describe results from some recent studies on this phenomenon.

Since migrations of freshwater fish often occur along narrow corridors, i.e., streams and rivers, they may be broken down by hydrological disruption, for example, dam building by humans. In such situations there is an excellent opportunity to compare biological dynamics in systems with and without migration. As a consequence of colonial dam building in New England lakes, several populations of previously anadromous alewives became landlocked, forcing them to complete their life cycle within the lakes (Palkovacs et al. 2008). This year-round presence has significantly altered the lake ecosystems owing to forage-driven trophic effects from the alewives. More specifically, the naturally occurring anadromous migration of juvenile alewives in autumn creates a temporal absence of a keystone zooplanktivore, leading to a re-emergence of large-bodied zooplankton, which are absent in lakes without migration, i.e., with landlocked populations of alewives (Post et al. 2008). Besides these direct ecosystem effects, the migration of the alewives also has a significant effect on the biomass of edible phytoplankton during the summer, which nicely illustrates the trophic cascade mediated by migration.

In the alewife example all individuals either migrated or stayed resident, but between-year variation in the timing and proportion of migrating individuals in partially migratory populations has also been predicted to affect the population structure and dynamics of lower trophic levels (Brodersen et al. 2008a). In the aforementioned Lake Krankesjön, we have shown that differences in timing of the return migration of the dominant zooplanktivore (roach) to the lake during spring affect the spring peak abundance and size structure of zooplankton (Hansson et al. 2007; Brodersen et al. 2011). The timing of zooplankton and intensity of zooplankton grazing pressure during spring affects the probability of grazing-induced limitation of phytoplankton, and thereby the likelihood of a spring clear-water phase (Scheffer 1990; Hansson et al. 2007). The presence of a spring clear-water phase is crucial for many shallow eutrophic lake ecosystems because it provides a window of opportunity for the establishment of submerged macrophytes (e.g., Van Donk and Otte 1996). It has been suggested that factors affecting the timing and fraction of resident–migratory zooplanktivorous fish may provide feedback loops affecting the resilience of alternative stable states (macrophyte-dominated versus phytoplankton-dominated) in shallow eutrophic lakes (Brönmark et al. 2010). Furthermore, a recent study on migration in tropical floodplains suggested that migration of benthivorous fish drove the presence and absence of submerged macrophytes because of differences in resuspension affecting turbidity and thus light availability (Mormul et al. 2012).

5.3. Eco-evolutionary effects

Since fish migrations can have strong effects on the ecosystem through multiple pathways, it is not surprising that these effects can change selection gradients both for the potentially migratory species, i.e., eco-evolutionary feedbacks, and for other species in the ecosystem, i.e., eco-evolutionary cascades. The probably best-known case of eco-evolutionary feedbacks in connection with migration is the adaptation to feeding on small-bodied zooplankton by landlocked alewives (Palkovacs et al. 2008). Here the alewives have adapted to a zooplankton community structure, which was created by their loss of migration (see above). This adaptation is apparent in decreased gill raker spacing (Palkovacs et al. 2008) and in body morphology (Jones et al. 2013). But the temporal variation in presence and absence caused by the migration is also likely to affect the selection gradients of other species present in the ecosystem. For example, Walsh and Post (2012) described how life-history traits in the water flea *Daphnia ambigua* Scourfield, 1947, a preferred prey of local zooplanktivorous fish, differ between lakes depending on fish migration, where *D. ambigua* from lakes with anadromous alewives grow faster, mature earlier, and produce more offspring than *D. ambigua* from lakes with landlocked alewives (Walsh and Post 2012). Besides such top-down eco-evolutionary effects, it can also be hypothesized that there are bottom-up effects of migration, both ecological and evolutionary, where temporal absence of prey affects their predators. However, such effects are still to be described.

6. Conservation issues

Migratory fish rely on multiple habitats and open passages to migration destinations. The conservation of migratory fishes hereby demands complex consideration to enhance the probability of completion of all life stages. Although migrant fish should be adapted to the varying conditions between environments along the migration route, combinations of habitat changes may restrict the probability of successful migration. Also, if the migration route includes several habitat types, the deterioration of any of these may have impacts on migratory populations and communities (Katano et al. 2006). Many freshwater fish migrate along streams and rivers and anthropogenic activities such as damming, irrigation, and dredging affect hydrological, biological, and

habitat prerequisites for migration (e.g., Lucas and Baras 2001; Thorstad et al. 2008). The conservation of migrating populations or species hereby relies on careful consideration of the impact of anthropogenic activities across habitats. Degraded migration routes or destinations can furthermore have selective powers within populations. In partially migrating populations where migration propensity is linked to individual phenotypes (e.g., Brodersen et al. 2012; Chapman et al. 2011c, 2012a), reduced migration possibilities would select against migratory phenotypes, with consequences for biological diversity in populations. The conservation of migratory fish populations can include conservation of threatened species, as well as phenotypic diversity within species, and should be pursued in light of the multiple habitats required for successful fish migration. Obviously, completely obstructive constructions, such as dams, prevent migrants from completing migration along their natural route. Upstream fish migration in watersheds containing such dams has been facilitated by the introduction of fish ladders. Fish ladders, however, only permit migration of fish that can overcome the very strong currents commonly produced and can even select for specific phenotypic traits within populations (Volpato et al. 2009). A more recently introduced alternative to fish ladders are the so-called fishways or bypasses, where streams are created to offer migrating fish an alternative passage up and beyond dams. Although these bypasses are created to mimic natural streams (e.g., Calles and Greenberg 2005), their efficiency is sometimes arguable. For instance, the downstream mouth of the bypasses are commonly and for logistic reasons situated quite far from the dam wall and major water flow. Consequently, fish may have trouble finding them. Also, the design of fishways should consider a variety of fish and movement performances, as not all fish species can utilise all fishway designs (Mallen-Cooper and Brand 2007). Fishways have nevertheless been shown to allow for fish population connectivity over dam obstacles (Wolfebaek et al. 2011), where they give a reasonable and promising tool for connectivity restoration attempts.

7. Conclusions and future prospects

To understand the evolution of migration in freshwater fish and to explain the multitude of migratory strategies they employ at different spatial and temporal scales, from long-ranging migrations over several years, seasonal migrations over smaller spatial scales, down to diel migrations between habitats within the system, it is clear that we need to consider migration as part of an adaptive strategy to maximize the lifetime reproductive effort of migratory individuals. In this framework, we have found it very useful to consider the costs and benefits of different strategies, and how these cost-benefit trade-offs change with habitat- and time-specific changes in selection pressures, to understand the evolution of different migration strategies. Especially, in our own studies we have found that the trade-off between predation risk and growth potential, as first developed theoretically by Werner and Gilliam (1984), is a useful concept for understanding seasonal migration in cyprinids in general, as well as explaining why some individuals migrate while others remain resident (e.g., Brönmark et al. 2008; Brodersen et al. 2008c; Chapman et al. 2011c; Skov et al. 2011, 2013). Predation-growth trade-offs have also been used to explain the diel and horizontal migrations of fish in deep-water lakes (e.g., Mehner 2012; Muška et al. 2013) and in the future we look forward to seeing these applied to other species and other migratory strategies as well.

If cost-benefit models provide an answer to ultimate “Why?” questions, we still need to consider the more proximate “Where?” and “How?” questions of fish migration, e.g., what migratory trajectories do fish use and what are the physiological and morphological adaptations that allow for the spectacular migrations in freshwater fish? With regards to migratory behaviour of freshwater fish (Where?), it has historically been studied using visible,

external tags, but in recent years telemetry has become a standard method for studying migration trajectories of individual fish (for a review see Lucas and Baras 2001). In active telemetry the position of the individual fish is actively tracked by the researcher, a time-consuming and costly method that provides detailed information on the migration patterns of only few individuals. An alternative is to build permanent arrays or recording stations placed along the migratory route that allow for continuous recording of the behaviour of a large number of individually tagged fish over large geographic regions. Technological development including miniaturizing tags, longer life span of batteries, and lower costs has fuelled this development. Another important development is the advent of tags that record and store information about changes in the tagged fish’s physiology, including heart rate – electrocardiogram (Muramoto et al. 2004), muscle activity (Quintella et al. 2004), acceleration (Nakamura et al. 2011), or a combination of these (Clark et al. 2010). Data storage tags (DST) can also sample information on different environmental signals in the vicinity of the tagged fish, including conductivity, temperature, oxygen, pressure (depth), light intensity, or salinity (e.g., Neuenfeldt et al. 2007; Aarestrup et al. 2009). DST tags are most often dependent on being retrieved from the tagged fish, which can be a challenge, but a recently developed alternative is the so called pop-up tags where the tag is released from the fish and float to the surface at a predetermined time or when the fish die (e.g., Aarestrup et al. 2009). After release, the tag uploads its stored data to a satellite from which it can be retrieved and used to infer, e.g., migration routes and habitat use. Clearly, the development of more sophisticated tagging technology has moved its use from mere description of migration trajectories to investigations of the physiological and morphological adaptations behind (i.e., “How?” questions).

Recent advances in molecular genomics have provided us with another excellent tool kit to understand the adaptations of migration and the genetic and molecular mechanisms behind. The studies reviewed above illustrate that migration as a trait is likely to be under some genetic influence. However, some of these studies also make it clear that it is often a problem to clearly separate the genetic and environmental components underlying a phenotypic trait.

The development of next generation sequencing now allows for the rapid generation of large amounts of sequence information from nonmodel species that can be used to create transcriptome-wide microarrays to study gene expression in relation to different migratory strategies. Clearly, future studies that investigate gene expression of migratory strategies will provide us with a large-scale perspective on the molecular mechanisms behind phenotypes, as well as an understanding of population-level differences owing to differences in selection pressures. Here, species that show partial migration are especially suitable for studies of the genetics behind migratory strategies, as we here can easily contrast individuals with a migratory versus a resident strategy. Important questions to solve are, for example, the importance of different sensory inputs for navigation, which is still a question under much debate. Studying which genes are up- or down-regulated at specific parts of the migratory cycle should provide more definite answers to the importance of the magnetic field, polarized light, or stars for large-scale compass navigation. Recent studies have already started to apply genomic methods to study which genes are involved in olfactory chemoreception in fishes (Hino et al. 2009), suggesting that we in the near future have a more complete understanding of the interesting and important questions on the mechanism behind location of natal streams in salmonids and the use of olfaction for orientation in other taxa as well.

An additional layer of complexity (and interest) in fish migration is that migrations are often social. Many fishes migrate in groups, and this social aspect of migration has been largely

unexplored by researchers, perhaps because of the logistical difficulties involved. How important are social interactions in shaping individual and collective movement decisions during migration? How important is social learning of migratory routes? Experimental studies in the laboratory have revealed many fascinating insights into collective movement in fishes (Ward et al. 2008; Herbert-Read et al. 2011, 2012). The challenge is to scale up to address mass migratory movements of fishes in the wild. This will require new technologies and innovative solutions (e.g., Faria et al. 2010). For now at least, the role of social interactions in fish migration remains a tantalizing mystery.

Traditionally fish migration studies has been observational, e.g., description of the specific migration patterns of a particular fish species, often with low replication because of logistic constraints. The other commonly used approach is investigating relationships between migratory patterns and different environmental factors. Clearly, we need to move from such descriptive and correlational studies to more hypothesis-driven research where specific predictions derived from theory are tested using manipulative experiments (see, e.g., Brodersen et al. 2008c). Development of new theory and modeling of migratory systems are instrumental. As emphasized by Cooke et al. (2008), we also need to leave the reductionist approach and instead integrate different disciplines, such as behavioural and population ecology, physiology, genetics, and functional genomics, to understand how different costs and benefits (predation risk, parasitism, harvesting, food availability, reproduction opportunities, etc.) shape the migratory strategies of individuals. Having gained these data on an individual level, the next challenge will be to translate this highly variable knowledge into population and community processes. We also need to apply our knowledge to anthropogenically driven changes in selection pressures and how these will shape fish migration in the future, e.g., in the face of global climate change (e.g., Martins et al. 2012).

One of the first things you note when you dive into the literature of freshwater fish migration is the complete dominance of studies on salmonids, especially on migration trajectories and different adaptations that facilitate a successful migration. This is of course understandable, given the conspicuousness of salmonid migration, as well as their economic importance. However, given that we now find examples of migration at different scales in an increasing number of taxa, it is of course highly important that we expand migration research and include non-salmonids to a larger extent. Furthermore, the development of new technology has resulted in an extensive and sophisticated toolbox that could be used in the study of fish migration, and there is no doubt that these developments have been crucial for recent advancements of the field. We can surely look forward to a refinement of our present technology also in the future, giving us an increased potential of understanding the details of the wonderful world of fish migration.

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